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SPECIES PROFILES LIFE HISTORIES AND ENVIRONMENTAL
REQUIREMENTS OF COASTA (U) MAINE COOPERATIVE FISHERY
RESEARCH UNIT ORONO M A SELLERS ET AL JUL 84

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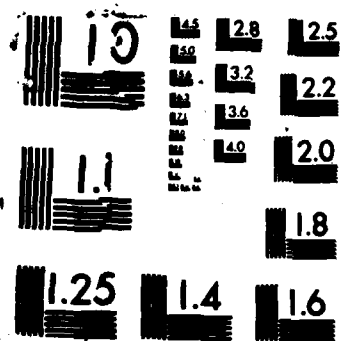
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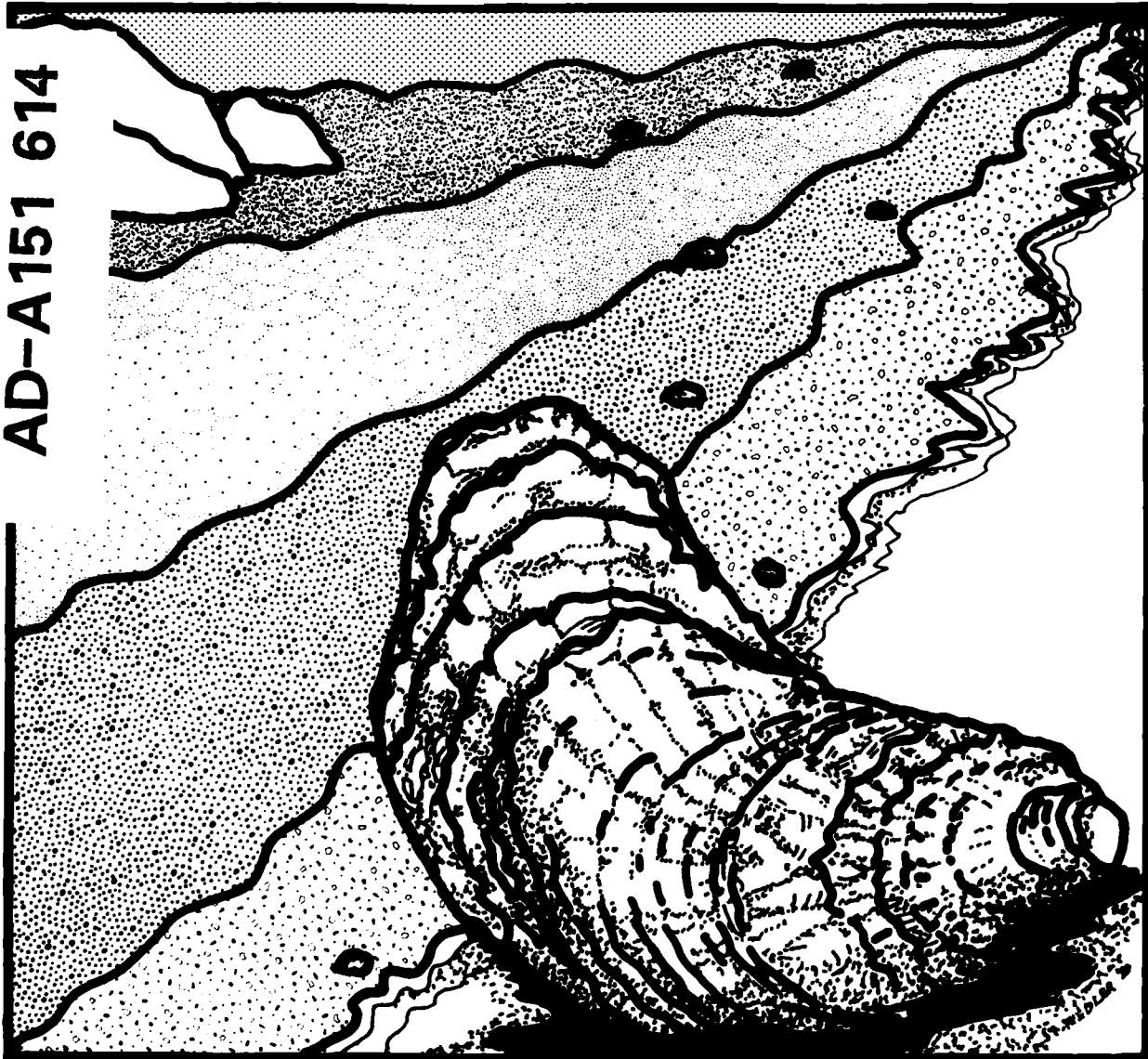
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**Species Profiles: Life Histories and
Environmental Requirements of Coastal Fishes
and Invertebrates (North Atlantic)**
AMERICAN OYSTER

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Species Profiles: Life Histories and
Environmental Requirements of Coastal Fishes and Invertebrates
(North Atlantic)

AMERICAN OYSTER

by

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Coastal Ecology Group
Waterways Experiment Station
U.S. Army Corps of Engineers
Vicksburg, MS 39180

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National Coastal Ecosystems Team
Division of Biological Services
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PREFACE

This species profile is one of a series on coastal aquatic organisms, principally fish, of sport, commercial, or ecological importance. The profiles are designed to provide coastal managers, engineers, and biologists with a brief comprehensive sketch of the biological characteristics and environmental requirements of the species and to describe how populations of the species may be expected to react to environmental changes caused by coastal development. Each profile has sections on taxonomy, life history, ecological role, environmental requirements, and economic importance, if applicable. A three-ring binder is used for this series so that new profiles can be added as they are prepared. This project is jointly planned and financed by the U.S. Army Corps of Engineers and the U.S. Fish and Wildlife Service.

Suggestions or questions regarding this report should be directed to:

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CONVERSION FACTORS

Metric to U.S. Customary

<u>Multiply</u>	<u>By</u>	<u>To Obtain</u>
millimeters (mm)	0.03937	inches
centimeters (cm)	0.3937	inches
meters (m)	3.281	feet
kilometers (km)	0.6214	miles
square meters (m ²)	10.76	square feet
square kilometers (km ²)	0.3861	square miles
hectares (ha)	2.471	acres
liters (l)	0.2642	gallons
cubic meters (m ³)	35.31	cubic feet
cubic meters	0.0008110	acre-feet
milligrams (mg)	0.00003527	ounces
grams (g)	0.03527	ounces
kilograms (kg)	2.205	pounds
metric tons (t)	2205.0	pounds
metric tons	1.102	short tons
kilocalories (kcal)	3.968	British thermal units
Celsius degrees	1.8(C°) + 32	Fahrenheit degrees

U.S. Customary to Metric

inches	25.40	millimeters
inches	2.54	centimeters
feet (ft)	0.3048	meters
fathoms	1.829	meters
miles (mi)	1.609	kilometers
nautical miles (nmi)	1.852	kilometers
square feet (ft ²)	0.0929	square meters
acres	0.4047	hectares
square miles (mi ²)	2.590	square kilometers
gallons (gal)	3.785	liters
cubic feet (ft ³)	0.02831	cubic meters
acre-feet	1233.0	cubic meters
ounces (oz)	28.35	grams
pounds (lb)	0.4536	kilograms
short tons (ton)	0.9072	metric tons
British thermal unit (BTU)	0.2520	kilocalories
Fahrenheit degrees	0.5556(F° - 32)	Celsius degrees

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We thank Dr. Herbert Hidu, Professor of Zoology, University of Maine, for reviewing the manuscript and offering many helpful suggestions.

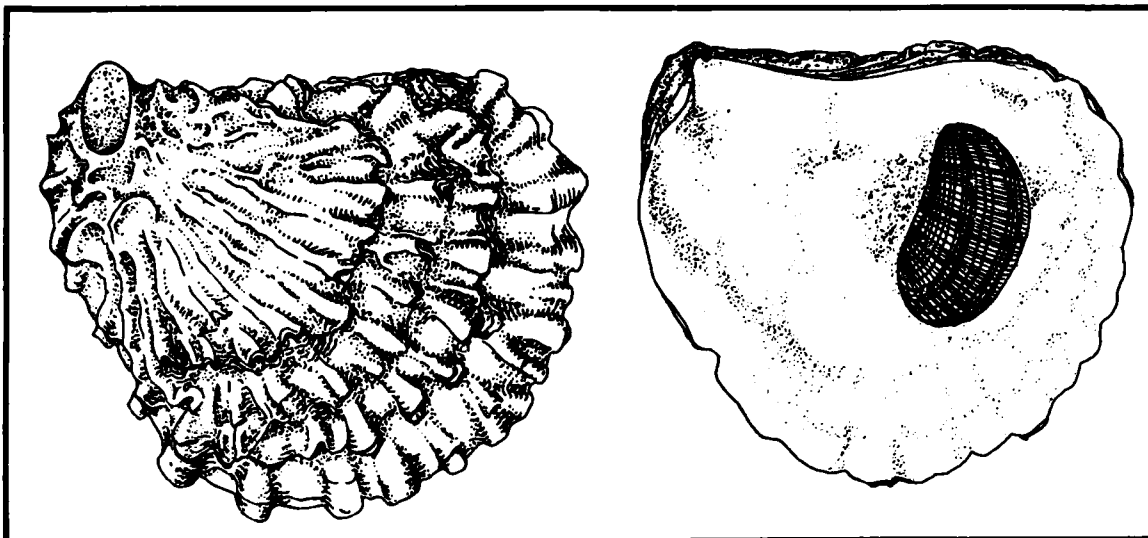


Figure 1. American oyster from Wellfleet Harbor, Massachusetts (Galtsoff 1964).

AMERICAN OYSTER

NOMENCLATURE/TAXONOMY/RANGE

Scientific name Crassostrea
virginica (Gmelin)
 Preferred common name . . . American
 oyster (Figure 1)
 Other common name . . . Eastern oyster
 Class Bivalvia (Pelecypoda)
 Order Pterioidea
 Family Ostreidae

Geographic range : In estuaries,
 drowned river mouths, and behind
 barrier beaches along the east
 coast of North America, from the
 Gulf of St. Lawrence, Canada, to
 Key Biscayne, Florida. In the
 Gulf of Mexico to the Yucatan
 Peninsula of Mexico, and in the
 West Indies to Venezuela. Intro-
 duced to Japan, Australia, Great
 Britain, Hawaii, and the west
 coast of North America (Ahmed
 1975). The largest American
 oyster populations are in the
 Gulf of Mexico, Chesapeake Bay,
 and Long Island Sound.

MORPHOLOGY/IDENTIFICATION AIDS

The left valve is almost always
 thicker and heavier than the right,
 and more deeply cupped (Yonge 1960;
 Galtsoff 1964). The oyster is cemented
 to the substrate on its left valve.
 Hinge teeth are absent, but a buttress
 on the right valve fits into a depres-
 sion on the left. There is no gap be-
 tween the valves when fully closed.

Shell shape is variable. On hard
 bottoms, beaks (umbones) usually are
 curved and point toward the posterior,
 whereas in silty environments or on
 reefs, umbones are usually straight.
 Single oysters from hard substrates
 are rounded and ornamented with radial
 ridges and foliated processes, whereas
 those from soft substrates or reefs
 are more slender and are sparsely or-
 namented. Shell thickness also depends
 on environment. Oysters on hard sub-
 strates have thicker and less fragile
 shells than those on soft substrate.
 The index of shape (height + width/

length) varies from 0.5 to 1.3 in southern populations and from 0.6 to 1.2 in northern populations.

Growth rings are oval with greatest growth along the dorsal-ventral axis. The principal growth axis is not permanent and may change several times over the lifespan of an individual, resulting in a zigzag pattern. The growth axis may change as much as 90°. Oysters 3 to 5 years old are usually 10 to 15 cm in height. Although tissue mass reaches an upper limit, the shell continues to grow over the lifespan of an oyster (Stenzel 1971). The largest height reported in the North Atlantic region is 35.5 cm, from the Damariscotta River, Maine (Galtsoff 1964).

The American oyster is isomyarian (adductor muscles are equal in size). The interior of the shell has a purple-pigmented adductor muscle scar situated slightly posterior and ventral. A second muscle scar, of the quenstedt muscle, is situated under the hinge. Chalky deposits may occur on the inside of the shell. The adductor muscle scar pigmentation distinguishes the American oyster from similar species. In C. rhizophorae and C. gigas the muscle scar is lightly pigmented, and in C. commercialis and C. rivularis it is unpigmented. Although C. gigas has been introduced to Salt Pond in Blue Hill, Maine, Wellfleet Harbor, Massachusetts, and Mobile Bay, Alabama, the only significantly numerous sympatric Crassostrea species is C. rhizophorae, which occurs along the southeastern and gulf coasts. The shell of C. rhizophorae is less plicated than that of C. virginica. Crassostrea species are distinguishable from Ostrea species by the presence of a promyal chamber, which is well developed in C. virginica. Crassostrea are oviparous, releasing gametes into the water, whereas Ostrea incubate fertilized eggs in the mantle cavity. Advanced Crassostrea larvae are distinguished from larvae of other bivalves by length-width measurements, and an asymmetric umbo. The dentition

on the hinge distinguishes larval C. virginica from other Crassostrea.

REASON FOR INCLUSION IN SERIES

American oysters support an important commercial fishery from the Gulf of Mexico to the Gulf of St. Lawrence, and are an important mariculture species. More U.S. plants produce oyster products than any other single fishery product, and over 10,000 people are employed in the oyster industry. Oysters are valued as a luxury food item. They are the keystone species of a reef biocoenosis that includes several hundred species (Wells 1961). Because oysters occur in estuarine areas, they are vulnerable to disturbance by development projects.

LIFE HISTORY

Spawning

Gametogenesis and spawning are stimulated by temperature (Hopkins et al. 1954; Kaufman 1978; Andrews 1979). The temperatures at which spawning occurs differ among populations. Stauter (1950) recognized three physiological races, two from the east coast and one from the gulf coast, which spawn at 16.4°C, 20.0°C, and 25.0°C, respectively. Evidence for physiological races was given by Loosanoff (1969), who found that gametes of 60% of the oysters from Long Island Sound populations ripened at 15°C after 45 days, whereas only 20% of the oysters from a New Jersey population had ripe gametes after 72 days at the same temperature. At 18°C none of the oysters from south of New Jersey matured, even after 3 years. The time required for gonad maturation (D) in Long Island Sound oysters is inversely proportional to temperature (T):

$$D = 4.8 + 4205 e^{-0.3554T}$$

Spawning may depend secondarily on tidal cycle; sunlight warmed water during low tide and stimulated spawning (Drinnan and Stallworthy 1979).

Spawning is initiated by one or more males, which release their sperm and a pheromone into the water. The females spawn when sperm enter the water transport system (Andrews 1979), or when pheromone stimulates females to release their eggs in a mass spawning (Bahr and Lanier 1981). Females produce 23.2 to 85.8 million eggs per spawning, with the number of eggs proportional to the size of the individual (Davis and Chanley 1955). Fecundities of 15 million to 115 million were cited by Yonge (1960). Females may spawn several times in one season, and the number of eggs produced is not proportional to the spawning interval. As spawning interval increases, obviously the number of eggs per season decreases (Davis and Chanley 1955). The spawning season is longer in warmer climates: from April to October in the Gulf of Mexico (Hayes and Menzel 1981); but from July to August in Malpeque Bay, Prince Edward Island (Kennedy and Battle 1963); and only in July at Sidedford River Estuary, Prince Edward Island, Canada (Drinnan and Stallworthy 1979). The egg stage ends at 6 hr after fertilization at 24°C (Loosanoff 1964).

Larvae

Oyster larvae are meroplanktonic, remaining in the water column for 2 to 3 weeks following fertilization (Bahr and Lanier 1981). During this period the larvae pass through several stages of development (Carriker and Palmer 1979). After the blastula (3.2 hr), gastrula (4.5 hr), and trochophore (10 hr) stages (Parrish 1969), the larvae secrete a straight-hinge shell and develop a ring of locomotory cilia called the velum. The swimming trochophore stage is reached in 6-8 hr (Andrews 1979). This prodissoconch I or straight-hinge larva is about 75 μ m in diameter. This stage is followed by

prodissoconch II, which is characterized by pronounced umbones. These larvae are vigorous swimmers with a pair of pigmented eyes and an elongate foot with a large byssal gland (Andrews 1979). These larvae are 0.30 mm in diameter (Galtsoff 1964).

Carriker (1951) found that younger larvae stay in the water column about 1.0 m below the surface. Older larvae remain near the bottom in the halocline of estuaries during flood tide and rise nearer the surface during the ebb tide, although Andrews (1979) questioned this finding. Haskin (1964) demonstrated that gradually rising salinities stimulate older larvae to swim and falling salinities cause them to sink. Hidu and Haskin (1978) observed spiral swimming during constant salinity, and linear swimming during gradually increasing salinity; swimming velocity increased by a factor of three at salinity near 100‰ seawater. Upward swimming is at nearly 1 cm/sec (Andrews 1979). These behavioral traits perhaps result in selective tidal transport and allow larvae to avoid being flushed from the estuary. Larvae may even be transported up an estuary (Seliger et al. 1982).

Juveniles

The larvae at 2 to 3 weeks after spawning seek a solid surface and commence a period of crawling in a circular area, presumably seeking a place for attachment (Andrews 1979). After attachment with a droplet of liquid cement exuded from a pore in the foot, they lose the velum and foot and are now called spat. Shells are preferred as attachment or setting sites, but stones and other surfaces may be used. Spat that set during the first 3 days after metamorphosis may grow faster than those setting later (Losee 1979). Metamorphosis may be delayed if suitable substrate is not present (Newkirk et al. 1977).

Several factors influence the setting behavior of larvae. Hidu and Haskin (1971) suggested that rising temperature over tidal flats during the flood tides stimulates setting. In the laboratory, rising temperature triggered setting (Lutz et al. 1970). Swimming larvae have positive phototaxis, which becomes negative with increased temperature (Bahr and Lanier 1981). More oysters settled in the subtidal zone than elsewhere in Delaware Bay (Hidu 1978). Setting was greater on shells at 2 m depth than on shells at 1.2 m or 0.3 m (Drinnan and Stallworthy 1979). However, Andrews (1979) observed more setting off the bottom, and attributed the opposite results to siltation in shallower water.

Oyster larvae set in established oyster beds. Crisp (1967) postulated that larvae are attracted to the proteinaceous surface of the periostracum of adult shells and observed that larvae do not settle on shells that had been treated with bleach. Hidu (1969) demonstrated, however, that a water-borne factor, perhaps a pheromone, is involved; larvae settle on oyster shells associated with existing oysters. Currents also influence setting patterns. Keck et al. (1973) found that setting in estuaries is heaviest on the eroding banks of tidal creeks.

Adult

Because adults are completely sessile, their distribution depends on where the larvae set and on subsequent mortality. Oysters typically occur in clumps called reefs or beds, in which they are the dominant organism. The mass of shells often results in alteration of currents and increased deposition so that the local environment is modified.

Adults are dioecious, but often change gender (Bahr and Lanier 1981). The gender and the process of sex inversion are genetically determined by perhaps three loci (Haley 1977).

Typically the young adults are predominately males; subsequent sex inversion with age increases the number of females. Sex ratios in the James River Estuary, Virginia, change from 90% males at 1 year of age to 80% females in older oysters (Andrews 1979).

GROWTH CHARACTERISTICS

Growth is greatest during the first 3 months, and spat reach 15 mm in 9 months (Bahr 1976). In their second year, juveniles that were 11 to 14 mm on April 3 were 18 to 22 mm on May 7, 23 to 27 mm on June 5, and 26 to 32 mm on July 2 (Carriker et al. 1982). Body weight increased from 0.23 g to 4.0 g during this 3-month period. Monthly shell increment ranged from 1 to 3 mm per month in South Carolina (Manzi et al. 1977; Manzi and Burrell 1977); or 20 mm per year in Maine (Price et al. 1975). Instantaneous monthly growth coefficients ranged from 0.42 to 0.84 (Gillmor 1982). The marketable size of 90 mm is attained in 3 to 5 years.

Growth is influenced by temperature, salinity, intertidal exposure, turbidity, and food. Growth is greatest in August and September after spawning, when glycogen reserves are restored (Loosanoff and Nomejko 1949; Price et al. 1975). Growth ceases during winter, except in Florida, where growth was continuous throughout the year (Butler 1952). Growth is slowed by spawning because energy is used for gamete production instead of production of body biomass. Butler (1953) noted a weight increase after spawning without an increase in length.

Fluctuating environments may promote better growth. Oysters in fluctuating salinity grow better than those under constant conditions (Pierce and Conover 1954). Oysters exposed during the tidal cycle grow about the same as those continuously submerged (Gillmor 1982). Long expos-

ure, however, reduced growth; those exposed 20% of the time grow twice as fast as those exposed 60% of the time. Growth rate is directly related to phytoplankton density, and some of the observed effects may be due to changes in phytoplankton. Manzi et al. (1977) observed that oysters grow faster in salt ponds than in tidal creeks, where primary productivity is lower. Crowding may prevent spawning and thus indirectly may lead to increased growth (Butler 1953).

Oysters over 200 mm long are not uncommon. A Walford plot of intertidal oysters predicts that oysters would cease growing at 140-mm length (Dame 1971).

COMMERCIAL HARVEST

The American oyster had traditionally supported a significant industry along the entire eastern seaboard. Today, there are only six commercial areas in the North Atlantic region (Figure 2). Domestic landings have decreased from about 100 million lb during the 1920's to 50 million lb during the 1960's, and have not recovered to the original levels (Table 1) (Matthiessen 1969). Although harvests in the Gulf of Mexico and South Atlantic have remained stable for the past 30 years, harvests in the mid-Atlantic and Chesapeake Bay have declined. In Long Island Sound, persistent set failure has been responsible for declining stocks. Although oysters spawn at the summer temperatures of the sound (20° to 21°C), setting must occur in warmer estuaries. Because of shoreline development, the amount of setting area has declined (Matthiessen 1969). Heavy mortalities due to the predatory starfish Asterias forbesi and the gastropod Urosalpinx cinerea in saltwater, and the predatory flatworm Stylochus ellipticus in brackish water, have also contributed to declining stocks (Matthiessen 1979).

Oysters are harvested in a variety of ways, including handpicking of clumps from reefs (Bahr and Lanier 1981), hand and patent tonging, and dragging from sailpowered craft in the Chesapeake Bay, and dredging from powercraft in Long Island Sound and (Korringa 1976).

The American oyster is also one of the predominant species used in mariculture, including in the North Atlantic region. In 1980 the yield of cultured oysters was 23,705,000 lb valued at \$37,085,000. This represents 55% of the total harvest of 42,439,000 lb. The equivalences between different values reported for harvest are: 1 bu = 34 l = 32 kg total weight = 7.8 pints = 3.4-kg meat weight (Pruder 1975).

The market quality varies with the season. The yield of meats is lowest in the summer months and peaks in March (Rockwood and Mazek 1977). This corresponds to a reduced-condition index following spawning (Hopkins et al. 1954; Lawrence and Scott 1982).

Population Dynamics

The enormous numbers of eggs and larvae produced by American oysters largely perish before setting. Following spawning, oyster larvae are common in the plankton, with numbers reaching 5,000 to 10,000/kl in Canadian waters (Drinnan and Stallworthy 1979) and 2,000 to 5,500/kl in Virginia (Andrews 1979; Seliger et al. 1982), with a peak in abundance after high tide (Andrews 1979). The daily mortality of larvae is 10% (Drinnan and Stallworthy 1979). Newly set spat had 79% to 99% mortality in 1 month in Massachusetts (Krantz and Chamberlin 1978). Spat mortality of 50% to 70% in Delaware Bay was reduced to 30% to 40% if spat were protected from predators (Tweed 1973). Spat survival was less in dense sets than in sparse sets in Chesapeake Bay (Webster and Shaw 1968). Annual changes in population density in Long

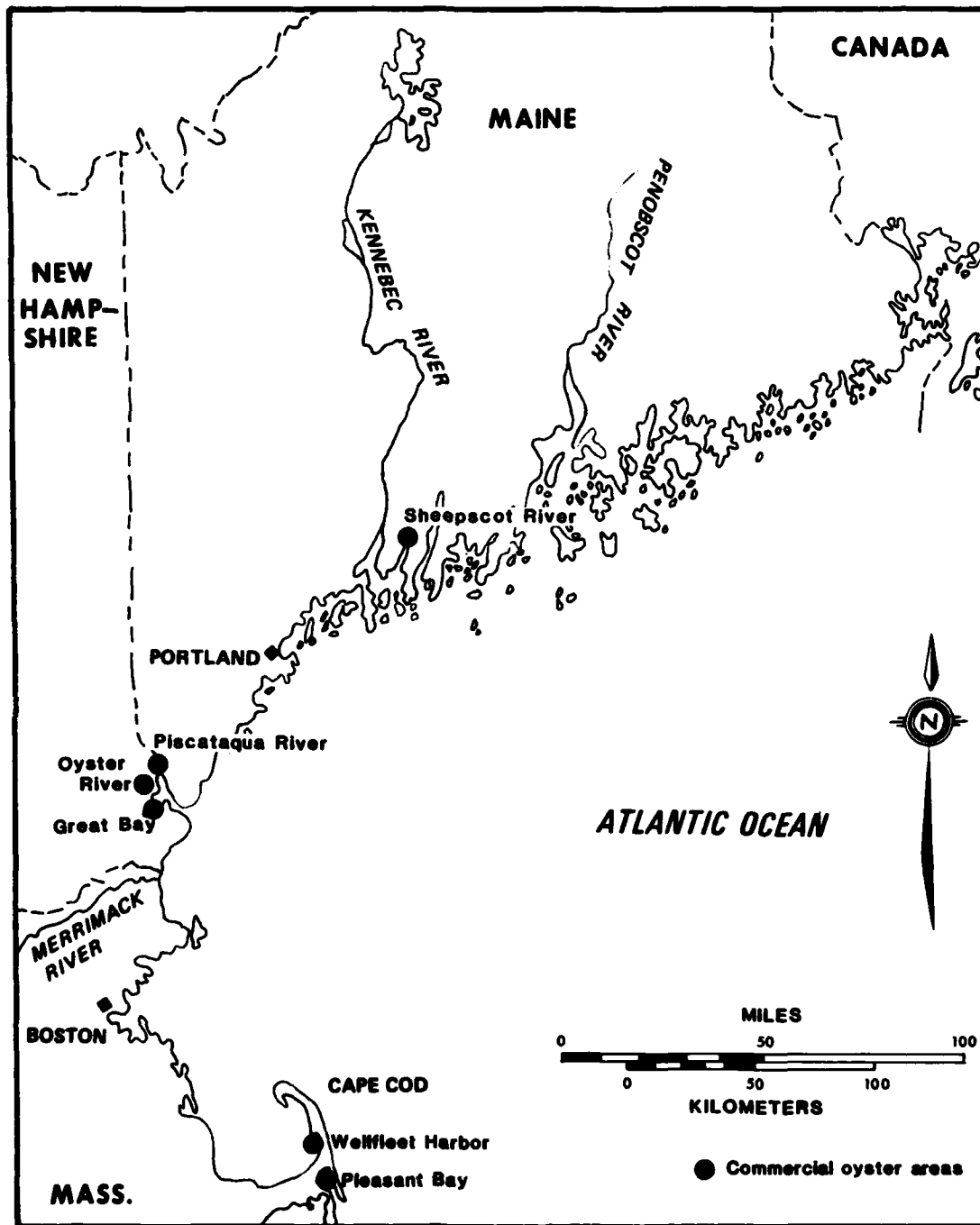


Figure 2. Recent commercial American oyster areas in the North Atlantic Region. Commercial harvest is now prohibited in Great Bay and is low in Pleasant Bay (Ralph Andrews, U.S. Fish and Wildlife Service, Newton Corner, Massachusetts).

Table 1. Oyster harvests (thousands of pounds meat weight) by geographical region for the years 1950-1980 (from various issues of Current Fisheries Statistics, National Oceanic and Atmospheric Administration).

Year	New England ^a	Mid-Atlantic	Chesapeake	South Atlantic	Gulf of Mexico
1950	4727	18170	29954	3033	12292
1951	1970	17410	29598	3783	11519
1952	2209	16767	34418	4111	14637
1953	1038	14462	36946	4019	12836
1954	745	13377	41587	3811	11443
1955	619	9848	39227	2260	13881
1956	506	8466	37064	3656	13513
1957	405	7981	34234	3069	14307
1958	276	4296	37530	2651	10408
1959	387	1392	33322	3516	13721
1960	500	1154	27111	4119	16098
1961	453	1921	27500	3984	18240
1962	294	2362	19939	3850	18838
1963	452	951	18274	4837	24139
1964	195	1356	22098	3527	23385
1965	340	757	21188	4082	19156
1966	N/A ^b	N/A	21232	3657	17182
1967	"	"	25798	3160	21747
1968	"	"	22679	2965	26739
1969	"	"	22157	1830	19765
1970	"	"	24668	1626	17714
1971	"	"	25557	1846	20266
1972	"	"	24066	1868	18260
1973	"	"	25400	1656	14914
1974	"	"	25021	1841	14878
1975	"	"	22640	1585	19295
1976	"	"	20964	1704	21569
1977	"	"	17929	1847	18081
1978	"	"	21531	2138	18212
1979	"	"	20428	2441	15289
1980	"	"	21906	N/A	N/A

^a Includes Connecticut and Rhode Island from the Mid-Atlantic Region.

^b N/A = Data not available.

Island Sound (MacKenzie 1981) suggest survival rates: spat occur at densities of 200 to 10,000/m²; 1- to 2-year olds at 300/m²; and 3- to 4-year-olds at 75/m². Adult survival in South Carolina was 85% in a salt pond and

94% in an estuary (Manzi and Burrell 1977). Survival was 100% in areas protected from wave action in North Carolina, and 50% per month if exposed to waves (Ortega 1981).

ECOLOGICAL ROLE

Larvae feed on plankton. Guillard (1957) observed that small, naked flagellates (chrysophytes) are the preferred food for larvae. Davis and Calabrese (1964) found that at low temperatures larval growth is best with a diet of naked flagellates; whereas at temperatures above 27°C naked algae do not survive and chlorophytes are a better food source. Larvae in turn serve as food for a wide variety of filter feeders (Andrews 1979).

The adults are important filter feeders in estuarine ecosystems and feed on naked flagellates in the 3- to 4- μ m size range (Haven and Morales-Alamo 1970). For each gram of dry weight of tissue, an oyster filters 1.5 l/hr, with a maximum of 1.9 l/hr (Palmer 1980). The filtration rate is independent of the algal food concentration in the seawater.

Oysters are the keystone species of a diverse community in the estuarine ecosystem. Bahr and Lanier (1981) reported the occurrence of 42 macrofaunal species or groups, and Wells (1961) listed 303 species associated with the oyster community. Because of their abundance, oysters are responsible for 87.5% of the respiration of an oyster reef (Bahr and Lanier 1981).

Oysters are subjected to a variety of diseases and parasites and support several predator populations (Galtsoff 1964). Bacterial diseases include *Vibrio* and *Pseudomonas* species. The fungus *Dermocystidium marinum* infects oysters in the southern range from Delaware to Mexico. The haplosporidian protozoan *Minchinia nelsoni* is responsible for the disease MSX (multinucleate spheroid unknown), and *Minchinia costalis* for SSD (seaside organism). *Minchinia nelsoni*, found from North Carolina to Massachusetts (Krantz et al. 1972), caused extensive oyster mortalities in the

Delaware Bay in 1957 and in Chesapeake Bay in 1960 (Andrews 1968). *Minchinia costalis* caused extensive mortalities in the seaside bays of the Delmarva Peninsula in 1960 (Rosenfield 1971).

Oyster predators include the gastropod oyster drills (*Urosalpinx cinerea* and *Eupleura caudata*), the whelk (*Busycon canaliculatum*), the starfish (*Asterias forbesi*), and the crabs (*Cancer irroratus*, *Callinectes sapidus*, and *Carcinus maenas*) (Galtsoff 1964). All oysters are susceptible to predation by oyster drills, which bore through the shells with a combination of chemical dissolution of the shell and drilling; but only smaller oysters are susceptible to predation by crabs and starfish. Widespread infestation also occurs from the boring sponge *Cliona*, which lowers quality. Oyster reefs may be smothered by excreta of worms of the genus *Polydora*. Juveniles are preyed upon by the flatworm *Stylochus ellipticus* (MacKenzie 1970).

Major competitors of the oyster include the slipper limpets (*Crepidula* sp.) and the jingle shells (*Anomia* sp.) as well as barnacles and other oysters that set on adult shells (MacKenzie 1970). The mussel (*Brachiodontes exustus*) may also compete with oysters (Ortega 1981).

ENVIRONMENTAL REQUIREMENTS

The American oyster typically lives in shallow, well-mixed estuaries, lagoons, and oceanic bays that fluctuate widely from hot to cold temperatures, low to high salinities, and clear to muddy waters (Andrews 1979). Because they live in such an extremely varied habitat, exact environmental requirements alone or in combination are difficult to define.

Temperature

Larvae do not tolerate as wide a range of temperatures as adults. Water temperatures of 30° to 34°C impair

growth, and even a brief exposure for 10 min at 40°C retards growth in Cheasapeake Bay (Hidu et al. 1974). The temperatures cited for fastest growth and highest survival, 27.5° to 32.5°C, in Long Island Sound (Davis and Calabrese 1964), seem a bit high.

Adults tolerate a water temperature range from -1.7°C in New England to 36°C in the Gulf of Mexico. Oysters may be exposed at low tide to temperatures below freezing or above 49°C (Galtsoff 1964). High temperatures increase the mortality rate; temperatures above 35°C for the whole tidal cycle caused death of some oysters (Tinsman and Maurer 1974). The critical thermal maxima for the American oyster is 48.5°C (Henderson 1929). Oysters tolerate freezing of their tissues, and revive after thawing (Loosanoff 1965a).

Optimum temperatures for adult American oysters are 20° to 30°C. Optimum temperatures for pumping were 20° to 25°C (Collier 1951). Growth ceased below about 8°C (Price et al. 1975). Oysters at 2° to 7°C remained inactive. Exposure to warm temperatures out of season stimulated growth if food was available (Ruddy et al. 1975). Growth is possible between 6° and 32°C with the optimum at 25° to 26°C (Galtsoff 1964). Exposure to 35°C water accelerated gametogenesis and spawning, but subsequent spawning was prevented (Quick 1971).

Differences in thermal requirements of oysters from different areas have led to the postulation of different races, each with different temperature requirements (Ahmed 1975). Spawning temperatures for three distinct races were reported by Stauber (1950) to be 16.4°C for the northern race (New England), 20.0°C for the mid-Atlantic race, and 25.0°C for the Gulf of Mexico race. Additional evidence for the existence of physiological races was reported by Menzel (1955), who found that ciliary activity continued at 0°C in northern

oysters but ceased at 6°C in southern oysters. Andrews (1979) believes there are other races as well. Genetic studies did not closely support the existence of physiological races. Buroker et al. (1979) found that all oysters studied were identical, except oysters from Nova Scotia and Florida. These populations were 82% similar, about the level of similarity between *C. virginica* and *C. rhizophorae*, which can successfully hybridize (Bahr and Lanier 1981). Oysters in Laguna Madre, Texas, however, are genetically distinct from four other gulf populations (Groue and Lester 1982). Measurement of isozymes in the genetic studies, however, may not indicate these races.

Salinities

Salinities above 7.5 ppt are required for spawning (Loosanoff 1948). Larvae tolerate salinities of 3.1 to 30.6 ppt (Carriker 1951), but grow fastest and survive best at salinities above 12.5 ppt (Davis and Calabrese 1964). Most larvae in a New Jersey estuary were in the halocline at salinities above 5 ppt (Carriker 1951). Optimum salinities for the growth of spat were 15 to 22 ppt (Chanley 1957).

Adult oysters tolerate a salinity range of 5 to 30 ppt, outside of which they discontinue feeding and reproducing. The optimum salinity range is 10 to 28 ppt (Loosanoff 1965a). Loosanoff (1965b) found that many oysters survive 3 ppt for 30 days. Large mortalities, however, have been associated with prolonged spring floods in the James River, Virginia (Andrews et al. 1959); in Mobile Bay, Alabama (May 1972); and in the Santee River, South Carolina (Burrell 1977). Salinities during these freshets were below 2 ppt. Oysters in Louisiana died after 14 days at 6 ppt (Anderson and Anderson 1975).

Low salinity inhibits gonadal maturation in oysters in Chesapeake Bay (Butler 1949) and Long Island

Sound (Loosanoff 1953). Reproductive failure may be a direct effect of salinity or might be caused by inadequate feeding at low salinity. Lowered salinity may benefit oyster populations by killing predators. Oyster drills and starfish cannot tolerate brackish water (Loosanoff 1965a).

Habitat

Oysters can grow equally well on rocky bottoms or on mud capable of supporting their weight. Soft muddy substrates may be improved by adding clam or oyster shells. Oysters from muddy substrates are more slender than those from hard substrates (Galtsoff 1964). Hidu (1978) found that oysters prefer to set on the bottom rather than on panels suspended in the water column, and are generally found subtidally in Delaware Bay. The preferred habitats in shallow estuarine waters include flats and offshore bars (Hidu 1968) and oyster reefs (Bahr and Lanier 1981). Maximum setting occurs on horizontal surfaces (Cline 1976).

Currents are important to American oysters. The volume of water immediately above an oyster bed must be renewed 72 times every 24 hr for maximum feeding; therefore, oysters require a moderate current (Galtsoff 1964). Tidal flows of 156 to 260 cm/sec or higher are needed for optimum growth (Veal et al. 1972). Turbulent currents, however, can damage shells from transported sand and pebbles (Galtsoff 1964). Although a velocity of 150 cm/sec caused unattached oysters to tumble along the bottom (MacKenzie 1981). They are found in greatest abundance in areas of scour where current keeps the beds free of sediment (Keck et al. 1973). Currents are also necessary for removal of silt and feces.

Distribution is strongly correlated with mean low tide (MLT) elevation in Great Bay, New Hampshire (Hardwick-Witman and Matthiesson 1983). There were $5.6/m^2$ at 0 m MLT

elevation, $2.0/m^2$ at 0.5 m, $0.4/m^2$ at 1 m, and none at 1.5 m.

Other Environmental Factors

Hourly oxygen consumption is 39 ml/kg for a whole animal or 303 ml/kg of wet tissue (Hammen 1969). Oxygen consumption increases with increasing temperature; Q_{10} values (the factor by which a reaction velocity is increased by a rise in temperature of $10^\circ C$) reported by Bass (1977) range from 1.2 to 2.3 for gill and 2.7 to 4.2 for mantle tissue. There is a strong interaction between temperature and salinity; oxygen consumption increases much more at high temperatures if the salinity is lower (Figure 3). Oysters are facultative anaerobes and are able to survive daily exposure. They can also survive anaerobically for 3 days following spawning (Galtsoff 1964). Oxygen consumption is zero with the valves closed (Hammen 1969).

Oysters are able to tolerate turbid water, but pumping rate decreases with increasing turbidity. Pumping rate can be reduced 70%-85% over the range 0 to 1 g/l, depending on the nature of the suspended sediment (Loosanoff and Tommers 1948). In natural environments, however, oysters grow better in the more turbid zones in oyster beds than in less turbid areas (Rhoades 1973).

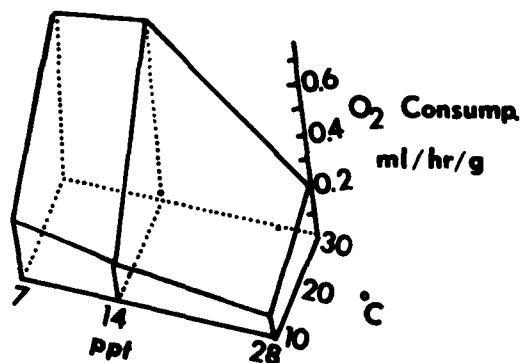


Figure 3. Oxygen consumption in American oyster as a function of salinity and temperature (Shumway 1982).

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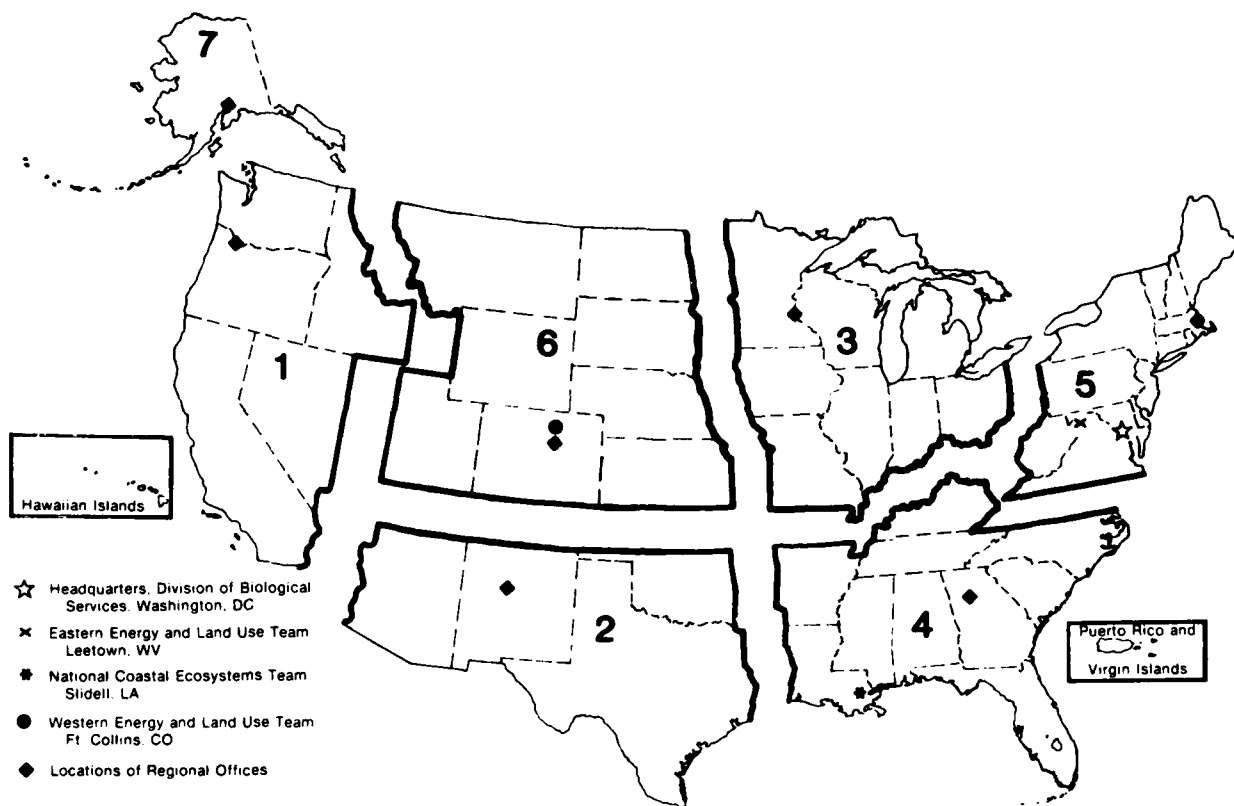
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16. Abstract (Limit: 200 words) Species profiles are literature summaries of the taxonomy, morphology, range, life history, and environmental requirements of coastal aquatic species. They are designed to assist in environmental impact assessment. The American oyster, <u>Crassostrea virginica</u> , is an important commercial and mariculture species. Spawning occurs repeatedly during warmer months with millions of eggs released. Embryos and larvae are carried by currents throughout the estuaries and oceanic bays where they occur. The few surviving larvae cement themselves to a solid object, where they remain for the remainder of life. Unable to move, they must tolerate changes in the environment that range from -1.7° to 49°C, 5 to 30 ppt salinity, and clear or muddy water.				
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